Explanation of Figures.

a, right upper molars; *b*, left lower molars.

Fig. 1.—*Eothenomys melanogaster confinii*, subsp. n. Type ♂. B.M. No. 22.12.1.1. Original No. 173. Kiu-chiang-Salween divide (*Forrest*). × 8.

Fig. 2.—*Eothenomys fidelis*, sp. n. Type ♀. B.M. No. 22.12.1.8. Original No. 455. Lichiang Range, Yunnan (*Forrest*). × 7·5.

Fig. 3.—*Eothenomys melanogaster colurnus*, Thos. ♀. B.M. No. 98.11.1.27. Kuatun (*J. de la Touche*). × 7.

Fig. 4.—*Eothenomys olitor*, Thos. (4 *b*, right lower molars). ♀. B.M. No. 11.9.8.123. Chao-tung-fu, Yunnan (*M. P. Anderson*). × 8.

Fig. 5.—*Eothenomys proditor*, sp. n. Type ♂. B.M. No. 22.12.1.10. Original No. 9. Lichiang Range, Yunnan (*Forrest*). × 7·5.

Fig. 6.—*Anteliomys wardi*, Thos. ♀. B.M. No. 22.12.1.30. Original No. 213. Mekong-Salween divide (*Forrest*). × 8.

Fig. 7.—*Caryomys inez*, Thos. ♂. B.M. No. 9.1.1.184. Shensi (*Malcolm Anderson*). × 8.

Fig. 8.—*Neodon sikimensis*, Hodgson. B.M. No. 15.9.1.218. Lachen, Sikkim (Bombay Nat. Hist. Soc.). × 8.

Fig. 9.—*Neodon forresti*, sp. n. Type ♂. B.M. No. 22.12.1.35. Original No. 145. Mekong-Yangtze divide (*Forrest*). × 9.

Fig. 10.—*Neodon irene*, Thos. ♀. B.M. No. 12.3.18.13. A-tun-tsi, N.W. Yunnan (*F. K. Ward*). × 8.

Fig. 11.—*Neodon carruthersi*, Thos. ♀. B.M. No. 9.4.3.93. Hissar Mts., Turkestan (*D. Carruthers*). × 8.

Fig. 12.—*Neodon oniscus*, Thos. Type ♂. B.M. No. 11.11.1.3. Kansu (*M. Anderson*). × 8·5.

Fig. 13.—*Microtus calamorum superus*, Thos. ♂. B.M. No. 11.6.1.46. Shen-Si (*M. Anderson*). × 8.

Fig. 14.—*Microtus clarkei*, sp. n. Type ♀. B.M. No. 22.12.1.46. Original No. 175. Kiu-chiang-Salween divide (*Forrest*). × 8.

XIII.—*The Dental Formula of the* Muridæ, *with especial reference to the* "mp. 4 *Theory*." By Martin A. C. Hinton.

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While working out a large collection together recently, Mr. Oldfield Thomas and I thought we ought to take the opportunity of expressing an opinion as to the notation that should be used for the three cheek-teeth of the Muridæ, *à propos* the formula used for certain voles by Mr. R. Kellogg *. Although Mr. Kellogg does not say how far the formula he uses should be applied to Muridæ other than voles, it is almost self-evident that any formula that may be applied to the voles must apply equally to the Muridæ at large. Having incurred a certain amount of responsibility in the matter, I had to prepare a statement of the theoretical questions involved for the use of my colleague; and in accordance with his desire that statement is recorded in the present paper.

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* Kellogg, "A Study of the Californian Forms of the *Microtus montanus* Group of Meadow-Mice," Univ. Cal. Publ. Zool. xxi. p. 245 (1922).

Kellogg's formula, viz., $p. \frac{4}{4}$, $m. \frac{1 . 2}{1 . 2}$, is identical with that used by Owen, who stated* that in the rodents "the first or anterior of the molar series, whether the number be 2—2, 3—3, or 4—4, is a premolar; it has displaced a deciduous predecessor in a vertical direction." But such a replacement is entirely unknown in Muridæ; and Owen's formula, lacking the support of any positive evidence, has been abandoned for many years in favour of that now in common use, viz., $m. \frac{1 . 2 . 3}{1 . 2 . 3}$.

So long ago as 1872, Forsyth Major† was led to suspect that the anterior cheek-tooth, above and below, in Muridæ is neither a "molar" nor a "premolar" in the ordinary sense of those terms, but is the posterior milk-molar, which in this family has become persistent in each jaw, the permanent premolar (*p.* 4), normally replacing this tooth, having been suppressed. Long afterwards, but independently, while working at Microtinæ, I arrived at a similar conclusion‡. Adopting Hensel's tooth notation (which personally I still prefer, although I realize that convenience now forbids its use), both Forsyth Major and I used for the the Muridæ therefore the formula $dm. \frac{1}{1}$, $m. \frac{1 . 2}{1 . 2}$, which in the more usual notation would be expressed as $mp. \frac{4}{4}$, $m. \frac{1 . 2}{1 . 2}$.

Kellogg cites the views of Forsyth Major and myself, but does not indicate clearly whether he intends to agree with us or not, although he seems to admit that the homologization of the front lower cheek-tooth in Microtinæ with mp_4 would afford an explanation of its complexity.

It is not possible in this place to present fully the case for the homologization of the teeth in question with $mp. \frac{4}{4}$; but a brief outline and a few facts in illustration of the argument are given in the following paragraphs. I would hasten to say, however, that although this homologization appears highly probable to me (and, I am permitted to say, not improbable to Mr. Thomas), both my colleague and I are strongly of opinion that the conventional formula $m. \frac{1.2.3}{1.2.3}$ should be adhered to, at least in ordinary systematic writing, until such time as definite proof of the "*mp.* 4 theory" can be supplied. Great difficulty and inconvenience arise in systematic work from too readily following unproved theories of tooth-homology*; and in the present instance, if it turn out that so important a change in the dental nomenclature of this great family becomes necessary, then the innovation should be made in a formal and conspicuous manner and not be merely indicated by eccentricities in the lettering of figures illustrating the teeth of some small local group.

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* Owen, 'Anatomy of Vertebrates,' 1868, vol. iii. p. 300.

† Forsyth Major, "Materiali," Atti Soc. Ital. Sci. Nat. xv. p. 112 (1872); "Nagerüberreste," Palæontogr. xxii. p. 75 (1873); "Fossilen Pferde," Abhandl. schweiz. paläontol. Ges. iv. p. 111, footnote 3 (1877).

‡ Hinton, Proc. Geol. Assoc. xxi. 1910, p. 490.

The argument in support of the "*mp.* 4 theory" may be shortly stated as follows:—In many Muridæ (and particularly among Microtinæ) the lower front cheek-tooth is extremely complex; to a lesser extent this is also true sometimes of its opponent in the maxilla (e. g., *Dicrostonyx*, *Eothenomys*, *Chiruromys*, and *Apodemus epimelas*). Wherever the available material permits us to work out the morphological history of the cheek-teeth, we find that within the Muridæ (and in nearly all the other rodents) a more complex condition of the crown is a primitive character as opposed to a more simple condition, which invariably appears to be the result of specialization. An enormous mass of facts might be cited in support of this statement, but it will suffice to say that clear evidence of the direction of dental progress, from the complex to the simple, in this family is afforded, firstly, by those very rare cases in which it is possible to trace a single phylum forwards in time (e. g., *Mimomys* in successive horizons of the Upper Pliocene and Lower Pleistocene of Britain); secondly, by the phenomena manifesting a progressive reduction and simplification of the cheek-teeth in the individuals of many species (e. g., *Arvicola amphibius*) as they pass from extreme youth to maturity; and, lastly, by many living and extinct genera in which the species seem to show a series of gradations from more primitive forms, with relatively complex teeth, to more specialized forms, with a simpler type of dentition. In the last class of case the personal equation is no doubt active; but the observer who has had training in dealing with cases of the first two classes runs comparatively little risk of inverting the sequence in cases of the third class. The principle involved in each of the three classes is one and the same. If, for example, we examine an absolutely unworn front lower cheek-tooth of *Mimomys* or *Arvicola* we find that it possesses a tubercular cap, reminiscent of the bunodont and brachyodont ancestors of the group; such a cap occurs, too, in the molars of most other rodents with "prismatic" patterns in the adults. In slightly deeper levels of the crown certain tubercles fuse together in such a way that when the tooth is worn down the characteristic prismatic pattern gradually comes into view. In an earlier species of *Mimomys* (e.g., *M. pliocænicus* we find that "m_1" (in the conventional sense) has three re-entrant folds upon its outer border for a considerable portion of the animal's life; but as middle age is approached the walls of the foremost fold knit together at a certain point—the inner part of the fold then being converted into an enamel "islet," while the outer part is represented by a vertical groove which channels the outer surface of the tooth. Gradually the "islet" and the groove die out in deeper levels of the crown, so that in old age, when wear is far advanced, all traces of these vestigial structures are lost. In later species (e.g., *M. intermedius*) exactly the same process, with exactly the same result, is seen—with a difference; the process is hastened, and the last traces ("islet" and external groove) of the third or front outer fold vanish before the animal is fully grown. In *Arvicola amphibius* and *terrestris* we have strictly parallel changes taking place upon the molar crowns within the first few weeks of the individual's existence; in these creatures there is a tubercular cap upon the summit of the tooth; then, in slightly deeper strata, the beginnings of those "prisms" and folds which form the characteristic pattern of the adult tooth, plus other prisms and folds, which, after lingering for a day or two, the transitory memorials of forgotten ancestors, rapidly disappear.

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* *Cf.* Thomas, Ann. & Mag. Nat. Hist. (9) ix. p. 671, footnote (1922).

By comparing the results obtained from the three lines of inquiry indicated above, it is possible to form an idea of the minimum amount of complexity which the cheek-teeth must have possessed in the most primitive Muridæ, or at least in those forms directly ancestral to the various living subfamilies. Investigations of this kind, involving the careful examination of many thousands of teeth, closely pursued for more than twenty years, have led me to infer that the anterior cheek-teeth in the ancestral Muridæ were multitubercular structures, consisting in the case of the lower tooth ("m_1") of at least twenty-one tubercles arranged in three longitudinal rows of seven each; and in the case of its opponent ("m^1") of at least fifteen tubercles similarly arranged in three longitudinal series of five each. The fate of these primitive elements has been various in the many subfamilies now recognized. In most groups they have suffered considerable numerical reduction (greatest perhaps in Gerbillinæ, least in Microtinæ); and this reduction has, in the normal mammalian manner, affected primarily the inner sides of the upper molars and the outer sides of the lower molars. More or less complete transverse fusions between the surviving tubercles of the three primitive longitudinal rows have taken place in all sections of the Muridæ, such fusions being most complete and most difficult to unravel in genera which have become completely hypsodont, though still apparent in many which have remained brachyodont. Far more important, the fate of the three longitudinal rows differs from section to section. In Murinæ, for example, the tubercles of the median row have grown at the expense of those forming the inner row in upper molars, the outer row in lower molars. In Cricetinæ, on the other hand, the tubercles of the median row are atrophied to a greater or less extent; sometimes to such an extent that even an experienced eye fails to detect the vestiges that usually remain. Lastly, in Microtinæ, the middle tubercles remain important elements, although fusions with those of the outer or inner rows and the general progress towards hypsodonty, which is so marked a feature in this group, have all but completely masked them as independent structures from our view. But, nevertheless, even in this subfamily, more or less clear traces of these median tubercles as recognizable elements of the molar crown are to be found occasionally: sometimes upon the unworn summits of the teeth, as in *Dicrostonyx*; sometimes regularly persisting in adult stages of wear, as in certain species of *Lagurus*; but most frequently cropping up as vestiges of peculiar form in slightly worn teeth, or recurring as atavistic abnormalities in the teeth of quite widely separated genera. In general, widely confluent opposed dentinal spaces (as in the teeth of *Evotomys*, *Eothenomys*, or the well known confluent pair of the "m_1" of *Pitymys*) may be taken as evidence of a relatively strong development of certain of the tubercles of the median row. Whether my estimate of the number of cusps primitively present be substantially accurate or not, there is, on the whole, abundant evidence that a high degree of complication must have characterized the anterior cheek-tooth in each jaw in the most primitive members of the family; and it is a complexity of which traces are retained to this day by many genera distributed among several of the most widely separated living subfamilies.

Our knowledge of Tertiary Rodentia is still very imperfect, for few have been discovered beyond the limits of Europe and America. On the other hand, those of Europe and North America are fairly well known. In the Tertiary strata of these two continents the Muridæ are comparatively poorly represented, and the known forms include none that can be regarded as even approximately representing the atavus of this great family. Upon reviewing all the molar types so far discovered among the earlier and middle Tertiary rodents, we fail to find one from which it would be possible to derive cheek-teeth possessing the complexity so characteristic of "m_1" and "m^1" in so many Muridæ, living and extinct, dating from the Pliocene period onwards—unless, indeed, we make the at present quite inadmissible supposition that new parts have been added to the teeth since the Miocene period. Such a supposition is inadmissible, firstly, because it would contradict all that we have learnt about the direction of dental specialization within the Muridæ from Pliocene times onward; and, secondly, because it would traverse the evidence of the older Tertiary rodents themselves. For even in the Eocene and Miocene periods rodent molars have generally undergone a process of progressive simplification (*e.g.*, Lagomorpha *); and to no order does Kowalevsky's famous comment ("Das kann schon als ein Wink dienen, wie weit wir noch von der primitiven Form des Zahnes sind, denn je tiefer wir in den Schichten dringen, je ältere Formen wir finden, desto complicirtere Gestalten tauchen immer auf"†)—uttered in another connection, it is true—apply with greater force.

The seeming impossibility of deriving these complex teeth from any known rodent permanent molar or premolar led, naturally enough, to the examination of the milk-dentition as the possible source of these organs. In most mammals the posterior milk-molars (and particularly mp_4) are commonly more complex than are either their vertical successors ($p.\,^4_4$) or the true molars ($m.\,\frac{1-3}{1-3}$) behind them. And among Tertiary rodents this is also sometimes the case, as, for example, in *Theridomys gregarius,* Schlosser, a Hystricomorph from the Oligocene of Quercy, in which species mp_4, when little worn, has an extremely complex crown of almost arvicoline aspect. The idea, therefore, of homologizing "m_1" and "m^1" of Muridæ with mp_4 and mp^4 of normal mammals presented itself successively, at widely different dates, to the minds of Forsyth Major and myself. Such homologies, could they be established, would do much towards bringing the Muridæ into line with other simplicidentate groups; and Forsyth Major, with characteristic insight and acumen, succeeded in showing that his theory was, at all events, not in conflict with the remainder of the evidence. He pointed out that:—

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* *Cf.* Forsyth Major, "On Fossil and Recent Lagomorpha," Tr. Linn. Soc. London, (2) vii. p. 433 (1899).

† Kowalevsky, "Anthracotherium," Palæontographica, xxii. p. 230, footnote (1874).

"Nager mit nur zwei ächten Molaren sind nichts Unerhörtes; im Oberkiefer von *Lagomys* z. B. haben wir drei Milchzähne, die gewechselt werden, und zwei ächte Molaren, im Unterkiefer zwei Milchzähne und zwei (beziehungsweise drei) Molaren. Dem vordersten Backzahn der Murinen geht kein anderer Zahn voran; daraus folgt aber noch nicht als Nothwendigkeit, dass es ein Molare sei; denn ein Milchzahn muss nicht nothwendig ersetzt werden" [*e.g.*, the foremost cheek-teeth in the horse and pig]. . . . "Der vorderste Zahn der Murinen hat die complicierte Gestalt des untern Milchzahns (d_1 [*i.e.*, mp_4]) von *Hystrix*, *Dasyprocta*, *Cœlogenys*, *Theridomys*, *Lepus* einerseits, sowie anderseits . . . . der grossen Mehrzahl der Placentalia überhaupt. Es wäre ohne die von mir vertretene Annahme auffallend, am Anfang einer Reihe von Backzähnen, die auf die geringe Zahl von drei reduciert sind, einen mehr als gewöhnlich ausgebildeten Zahn zu finden, während sonst grade reducierte Zähne die Reihe beginnen. Die Erscheinung findet ihre naturgemässe Erklärung, wenn wir annehmen, dass der unter (beziehungsweise im Oberkiefer über) *d.* 1 [*i.e.*, *mp.* 4] wegziehende Nagezahn die Entwicklung des Ersatzzahns *p.* 1 [i.e., *p.* 4] gehindert, grade dadurch aber zugleich indirect gewissermaassen fördernd auf die Entwicklung des Milchzahns eingewirkt hat, welchem letztern eine längere Existenz gesichert ist, weil kein Ersatzzahn sich unter ihm bildet, und somit kein Druck auf ihn ausgeübt wird. Unter Nagern ist die Zahnreihe am vollständigsten bei *Lepus,* bei welchem die Nagezähne am kürzesten sind und darum mit der Backzahnreihe in keinerlei Berührung kommen.—Wenn der Nagezahn mit seinem offenen Ende immer mehr von innen nach aussen vorrückte, so würde er schliesslich auf den Milchzahn (*d.* 1 = *mp.* 4) die gleiche Wirkung wie ein Ersatzzahn ausüben, d.h. sein

Ausfallen veranlassen. Nun stellen aber die Nagezähne junger Individuen Segmente eines viel kleinern Kreises der als die älterer, so dass sich also der Nagezahn bei zunehmendem Alter mit dem offenen Ende von seinem Platz unter- beziehungsweise oberhalb des *d.* 1 (*mp.* 4) nach hinten zu entfernen kann. Seiner Wirkung mögen wir dann in manchen Fällen die Verkümmerung des letzten Molaren zuzuschreiben haben, wie sie beispielsweise bei *Mus* vorkommt.—Ich prätendiere nicht, mit den vorstehenden Bemerkungen meine Ansicht bewiesen, glaube sie aber besser motiviert zu haben, als die allgemein herrschende es ist. Die definitive Antwort auf diese und ähnliche Fragen dürfen wir wohl mit der Zeit von der Palæontologie erwarten." ('Fossile Pferde,' p. 111, footnote.)

Two other little facts—trifles in themselves, no doubt—are worthy of note for the cumulative effect of their evidence. In South America, as Winge records (and as I have seen in a specimen from Cordova), the atrophy of the posterior molars in *Mus musculus* proceeds sometimes to the total suppression of those teeth; in Europe *m.* $\frac{3}{3}$ seem to be constantly present. Secondly, in those very rare cases in which an extra tooth is developed in Muridæ it appears at the posterior end of the series (*Microtus agrestis*, Winge; *Saccostomus hildæ**, B.M.); this extra tooth would have to be *m.* 4 according to the current notation, but it finds a perfectly natural explanation as *m.* 3, sporadically and atavistically returning, according to the *mp.* 4 theory.

To conclude, definite proof of the homologization of the teeth in question with *mp.* $\frac{4}{4}$ is not yet forthcoming; and it cannot be expected until palæontological research brings to light really primitive Muridæ from some still unknown old Tertiary horizon, possibly in south-eastern Asia. At present the Microtinæ seem to be the group most likely to afford the desired information; but nothing is yet known of the history of that subfamily before the middle or the late Pliocene. Of the species then existing some belong to still living genera and are dentally, at all events, as highly specialized as are their living representatives; others are, in a measure, primitive, but even they have proceeded too far along the path of dental progress to show us more than the direction of that path and its later portions. Such facts indicate clearly how far we are from the beginning of the

* Schwann, P.Z.S. 1906, p. 110.

story upon which the solution of this and many other interesting problems depends. But, whether this leads us to the ultimate acceptance of the *mp.* 4 theory or not, I can only reiterate my opinion that, in systematic writing, no change in the commonly accepted notation of the cheek-teeth of Muridæ should as yet be adopted.

XIV.—*The Godman Exploration Fund: List of Mammals from North Queensland collected by Mr. T. V. Sherrin.* By OLDFIELD THOMAS.

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IN this, the first paper dealing with the results of the Godman Exploration Fund, I may put on record that, as a peculiarly suitable memorial to her late husband, the well-known naturalist Mr. F. DuCane Godman, F.R.S., Dame Alice Godman has founded an Exploration Fund for the employment of zoological collectors to obtain specimens for the National Museum. The Trustees of the Fund will be a permament body, who will be glad to take charge of and utilize for the benefit of the Museum any further sums which patriotic persons may like to give or bequeath for the purpose of similarly benefiting the Museum collections.

By the help of the Fund, Mr. T. V. Sherrin has made a collection of Mammals in the district of Ravenshoe, North Queensland, south-west of Cairns, about 17° 40′ S. and 145° 30′ E., and these prove to be of so much interest as to deserve a special list. All are presented by the Godman Exploration Trustees to the British Museum.

Among them attention may be drawn to the well-marked species of Marsupial Mouse, which I have named after Mr. Godman *Phascogale godmani*, and to the little Platypus, which seems to represent a peculiar diminutive northern race of *Ornithorhynchus anatinus*.

In addition to the species here recorded, examples believed to be referable to *Æpyprymnus rufescens*, *Pseudochirus herbertensis* and *peregrinus*, *Petauroides volans*, and *Trichosurus vulpecula* were obtained, but, owing to various Customs' formalities, have not yet been received.

1. *Eptesicus pumilus*, Gray.

♂. 53, in spirit. Dinner Creek, Ravenshoe. 2900′.